

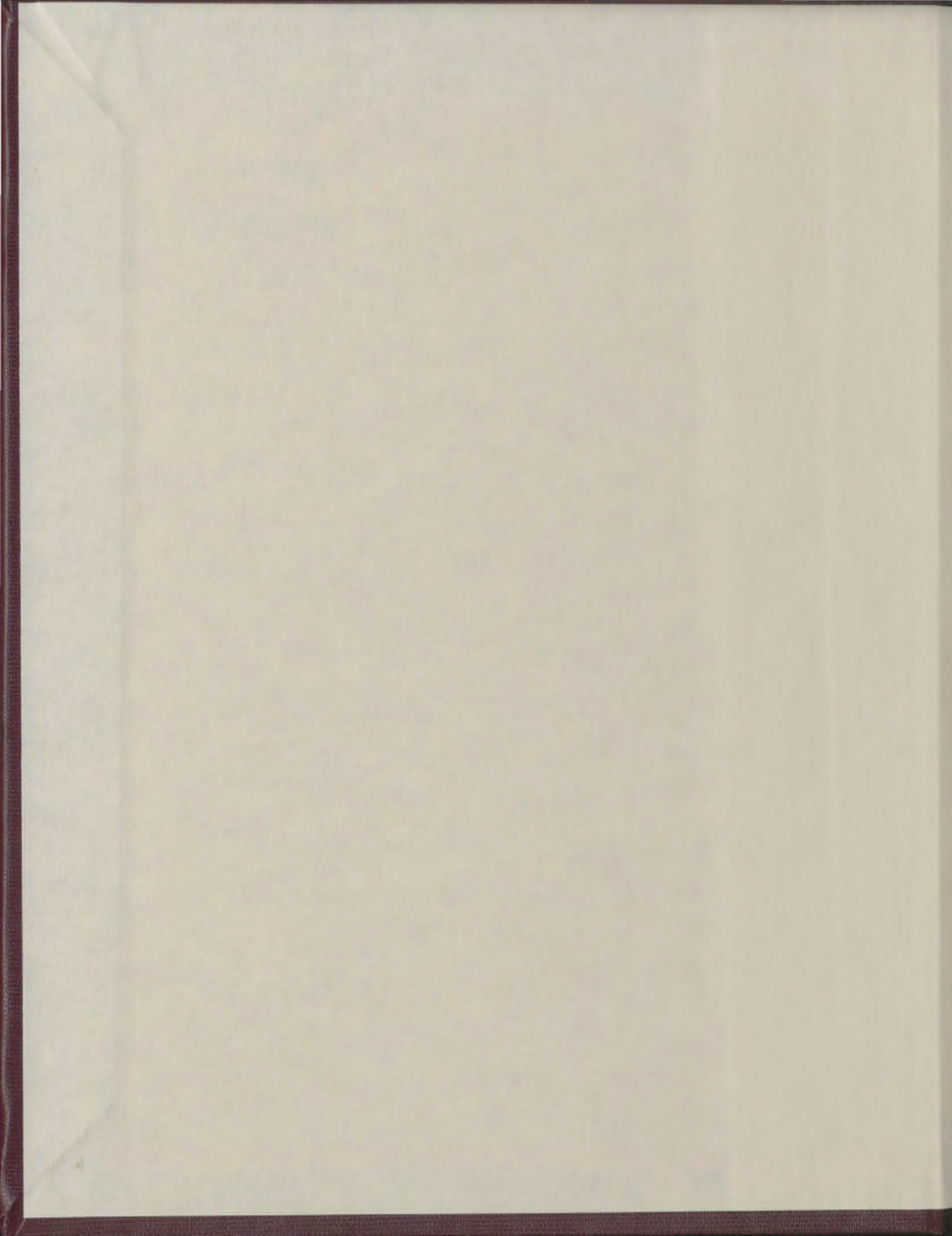
**A STUDY OF ACTIVITY, SOCIAL INTERACTION
AND SLEEP IN A CAPTIVE BREEDING
COLONY OF HARBOUR SEALS**

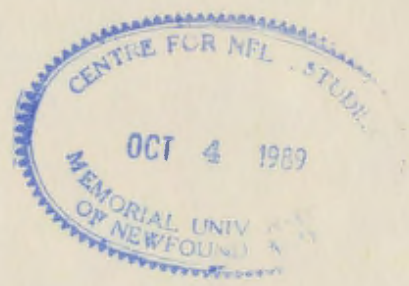
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ISBN 0-315-45094-0

**A STUDY OF ACTIVITY, SOCIAL
INTERACTION AND SLEEP IN A
CAPTIVE BREEDING COLONY OF
HARBOUR SEALS**

by

© **Mary Patricia Almon, B.A., B.Sc. (Honours)**

A Thesis Submitted to the School of Graduate Studies in
Partial Fulfilment of Requirements for the Degree of
Master of Science

Departments of Biology and Psychology
Memorial University of Newfoundland
May, 1988

ABSTRACT

Because harbour seals (*Phoca vitulina*) spend more than half their life at sea , researchers have not been able to observe much of their behaviour. The present study of a captive breeding colony of harbour seals explored the relationship between activity, social interaction, and sleep. Activity patterns for all five animals varied over the season (July 27, 1986 to October 25, 1986) as well as during the day. Adult animals were significantly more active than younger animals. A circadian activity rhythm was found in all seals with most activity occurring during the day. Although the animals in this study were given free access to food, the daily amount they ate varied over the season. As activity increased for both adult males, food consumption decreased. The female and younger animals showed no such activity changes as a function of appetite.

Copulation was witnessed on three occasions in August. Prior to mating, both adult males engaged in flipperslapping and bubbleblowing . After mating, these behaviours rarely occurred. The use of "space" by both adult males was restricted before mating but this disappeared after mating was over. Sleep varied over the observation period. No sleep was observed in any seal before mating, however, a marked increase occurred after the mating period. No significant differences were found between animals with respect to sleep in the water, however differences did occur between seals sleeping on land. Scanning only occurred on land, never in the water. Individual differences in scanning rates were found among animals.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Deane Renouf for her support and guidance during the writing of this thesis.

A number of persons deserve a special thank-you for their help and assistance; Dr. R. Khan for letting me occupy his laboratory and also for helpful comments and suggestions on thesis drafts.

Elizabeth Noseworthy for her assistance with videotaping and in helping me get started.

Abe Ross for his numerous tutorials on Time Series Analysis.

John Read at Computing Services for his assistance with the data.

The members of my thesis committee, Drs. Dale Corbett and Joe Brown for their helpful comments and suggestions.

Jack Lawson for his help in getting me started and familiarizing me with computers and SPSSX.

Dr. Graham Skanes for his helpful advice with the data.

Lachlan MacQuarrie for his helpful suggestions and especially for moral support.

I would like to extend a special thank-you to a good friend Bryan Acton. His time and assistance in data analysis was invaluable. Thank-you for making the analysis fun Bryan!

Finally, I would like to thank my family for their continual support and encouragement throughout all stages of this thesis.

Financial support was kindly provided by a Memorial University Of Newfoundland Graduate Fellowship and Bursary.

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Chapter 1

INTRODUCTION

Because harbour seals (*Phoca vitulina*) spend more than half their life at sea, researchers have not been able to observe much of their behaviour. These seals are monomorphic and difficult to capture for tagging, so proper documentation of the behaviour of known individuals has not been possible. Captive animals can be easily identified, therefore certain aspects of their behaviour can be measured precisely. This study of a captive breeding group of harbour seals focused on three aspects of their behaviour which have not been adequately quantified before; 1) Locomotor activity 2) Social interactions and 3) Sleep. It was hoped that this work would generate hypotheses which could be tested on a wild population.

Harbour seals copulate and feed in the water, giving birth on land to a pup which accompanies its mother to sea shortly thereafter. This is in contrast to grey seals (*Halichoerus grypus*) and elephant seals (*Mirounga spp.*) which remain ashore and fast during the entire breeding season. As a result, these animals are much more accessible than harbour seals, and some relationships between their reproductive behaviour and lactation and pup growth have been ascertained. For example, it has been shown that female grey seals increase their daily energy use by a factor of six during lactation (Fedak and Anderson, 1982). Similar measures have not been made with harbour seals, though the metabolic consequences of thermoregulation and swimming have been investigated (Davis, Williams, and Kooyman, 1985) as well as some metabolic effects of feeding (Ashwell-Erickson, and Elsner, 1981). However, the energy costs of their behaviour cannot even be approximated because most behaviour is out of view, and because basic activity patterns, which are important from an energetics perspective, have not been described.

Energetics are crucial for our understanding of the adaptive consequences of behaviour, since they provide direct measures of behavioural cost. However, until fundamental data, such as descriptions of activity and sleep cycles in and out of water are available, the costs and hence functions of these events will remain unknown. For example, it is not clearly understood why harbour seals spend time together out of the water. Though some workers feel they do so to rest and repay the energetic debt of movement and thermoregulation (Schneider et al, 1980), others hypothesize it is to share the burden of monitoring for predators (Terhune, 1985) while others suggest it is related to the spatial arrangements of their social organization (Davis and Renouf, 1987). If daily activity budgets are known, energy expenditure could be estimated, and some reasons for leaving the water might become clear.

Normally, wild animals will not breed in captivity (Haupt and Wolski, 1982) so laboratory observations of their behaviour may not be indicative of what occurs in the field. At the Marine Sciences Research Laboratory, there is a small colony of harbour seals which has recently become reproductive. Though their behaviour is bound to be altered by captivity, their production of young suggests that stress is not excessive, and that their behaviour might be closer to normal than that of a nonbreeding captive group. Therefore, it was worthwhile to examine quantitatively aspects of the behaviour of the MSRL colony, since detailed information has not been possible to gather in studies of this species to date. With these data, hypotheses about the function of various behaviour patterns might be developed.

1.1. LOCOMOTOR ACTIVITY

One objective of this study was to describe the relationship between activity, proportion of time hauled-out, and amount of food eaten. Some measurements of activity budgets have been made in other Phocids. Boness (1984) found that male grey seals spend approximately 88% of their time resting while Sandegren (1976) reported that northern elephant seals rest for approximately 95% of the time during the breeding season. Boness (1984) also reported that southern male

elephant seals exhibit an increase in activity prior to mating with the most active males having the greatest copulatory success.

The relationship between activity and food intake is important from an energetics perspective. The amount harbour seals eat has been indirectly estimated at 6-8% of total body weight daily. However, there appears to be significant variation in food consumption over the year (Spalding, 1964; Sergeant, 1973; Geraci, 1975; Boulva and McLaren, 1979). Ashwell-Erickson and Elsner (1981) reported that captive harbour seals ate more in winter than in summer but found no relationship between activity and food consumed. Similarly, Spalding (1964) suggested that feeding is minimal over the summer in this species.

A number of Phocids fast or show a reduction in food intake during pupping, breeding, and moulting seasons. Southern *Mirounga leonina* and Northern elephant seals *Mirounga angustirostris* mate on breeding beaches where adult males remain ashore for eight weeks or more. Females join the males for four to five weeks to birth and nurse their pups, mating just before returning to sea. Of necessity during this period the animals fast, as they do again when they later haul out for a few weeks to moult (Bartholomew, 1952; Laws, 1953; Carrick et al, 1962; LeBoeuf and Peterson, 1969; LeBoeuf, 1974; LeBoeuf and Briggs, 1977; McCann, 1983). Similarly, grey seals *Halichoerus grypus* copulate on land and remain on breeding beaches for weeks without feeding (Coulson and Hickling, 1960; Boness and James, 1979; Bonner, 1981). In spite of this reduction in feeding, the breeding season is a time of high energy costs for these species. Their expenditure is increased several times during their lengthy stays on pupping and mating grounds (Fedak and Anderson, 1982; Anderson and Fedak, 1985). Those males who are larger and have greater fat stores enjoy greater reproductive success (Anderson and Fedak, 1985).

The captive colony of harbour seals at MSRL are given free access to food, however they show periods of hyperphagia and hypophagia, occasionally eating nothing for days at a time. The species that copulate ashore are forced to fast by their long stay on land, but it is not understood why the other Phocids alter their food intake even though they spend part of every day in the water. It is possible that there are changes in the animals "motivational state" such that eating may

compete with other more important activities such as reproductive displays during the breeding season. The events leading to altered food consumption in the captive group may shed some light on the reasons for changes in the amount eaten by wild animals. In this study where behavioural activity and food intake could be monitored continuously, the relationship between particular types of activity and food consumption could be measured precisely.

1.2. SOCIAL INTERACTION

There are costs associated with inter-male competition in polygynous mammals, sometimes as serious as injury or death (Wilkinson and Shank, 1976; Clutton-Brock et al, 1979). Many species become hypophagic during the breeding season, diverting much of their energy into reproductive displaying, (eg: red deer, (Mitchell et al, 1976)). The consequences of social display and competition in harbour seals are not clear since the events preceding copulation have not been observed. Behaviour thought to be precopulatory has been loosely described in the literature, but mating itself has never been definitely seen in the wild. VENABLES and VENABLES (1959) reported that male harbour seals engaged in aquatic displays such as flipper splashing and bubble blowing. These displays occurred most frequently in July and August and coincided with weaning and breeding.

Much of the literature pertaining to harbour seal social behaviour remains speculative, since investigations of marked individuals have not been possible. Even if seals could be individually recognized, the majority of their social behaviour pertaining to mating occurs at sea and out of view. There is some controversy in the literature regarding the extent of harbour seal social organization. Some have described them as loosely gregarious animals on land (SCHEFFER and SLIPP, 1944; BISHOP, 1967; BUTTON, 1975) while others have speculated that they haul-out in socially structured groups (DAVIS and RENOUF, 1987; WILSON, 1978). It has been suggested that male harbour seals form dominance hierarchies (SULLIVAN, 1981) but do not compete for access to reproductive females (WILSON, 1978). STIRLING (1975) proposed that male Weddell seals *Leptonychotes weddelli* defend underwater territories, however there is no evidence to suggest that harbour seals or other species establish aquatic territories.

In this study, all of the events surrounding copulation could be observed and quantified in detail not possible in the field, in the hopes that new information would be provided about social behaviour in these seals.

1.3. SLEEP

A third objective of this study was to determine how much time harbour seals spend sleeping in water and on land since it has been proposed that the reason they come ashore is to sleep (Schneider et al, 1980). Seals can sleep both on land and in the water. In the water, they can do so totally submerged, or with their heads just above the water's surface. In the former instance they awaken every five minutes or so to surface and breathe (Ridgway et al, 1975). Although the stages of sleep in seals are the same as those seen in terrestrial mammals, some order differences exist. In terrestrial mammals, rapid eye movement or (REM) sleep is preceded by slow wave sleep (SWS). It is characterized by irregular heart rate and respiration. The opposite has been reported for Grey seals *Halichoerus grypus* (Ridgway et al, 1975). Ridgway et al (1975), using radiotelemetric devices, found that REM sleep in these animals preceded SWS and that it was characterized by a rapid, regular heart beat and regular respiration. Periods of REM sleep varied from 5 minutes to 63 minutes (Ridgway et al, 1975). Harbour seals in northern California *Phoca vitulina richardsi* spend 69% of their time sleeping and 12% in alert behaviour while on land (Sullivan, 1979). Mukhametov et al, (1982) examined sleep in Caspian Seals *Phoca caspica* over the summer and found that wakefulness occupied 85% of their daily cycle, slow-wave sleep 13%, and REM sleep 2%. They also reported that respiration could occur without awakening during slow-wave and REM sleep if the seal was sleeping at the water's surface or on land.

It is well documented that if mammals are deprived of sleep, or even just REM sleep, pronounced behavioural changes occur such as anxiety, irritability and an impaired ability to concentrate (Hartmann, 1973). Ridgway et al (1975) found that grey seals *Halichoerus grypus* REM sleep on land and in the water, but never underwater. Although Ridgway et al (1975) have reported that seals can

sleep with noses in air at the water's surface, rough weather and wind may prevent seals from keeping their heads above water, thus preventing them from entering REM sleep. Therefore, during inclement weather harbour seals may haul-out to REM sleep.

Schneider et al (1980) hypothesized that harbour seals haul out to sleep and conserve energy. Terhune (1985) has suggested that they haul-out to share the burden of watching for predators. Seals, when on land, visually scan the surrounding area every few minutes. The seal raises its head above a resting position or turns it to one side. Terhune (1985) found that as group size increased, vigilance (measured as scanning rate) decreased. He suggested that the seals took advantage of the larger numbers of watchers to spend more time resting and less scanning, supporting Schneider et al's (1980) contentions. However, Renouf and Lawson (1985) found overall vigilance rates increased for adults and juveniles as the breeding season progressed, with adult males showing a more pronounced increase than adult females. Vigilance increased with group size only for adult males.

Seals may show scanning rates on land which are the same as rates of waking when asleep underwater and are perhaps a consequence of the same mechanism. If seals spend a large proportion of their time in REM sleep when on land, rates of waking would be different than those seen when these animals sleep underwater. In this study, scanning and sleep rates as a function of seals location were compared to provide information about some of these questions.

Chapter 2

METHODS

2.1. SUBJECTS

The subjects were nine captive harbour seals housed in an outdoor holding tank (7.62m diameter, 1.37m deep) at Memorial University's Marine Sciences Research Laboratory, Logy Bay. Six of the nine harbour seals were from Sable Island or Miquelon, (45° 45' N, 56° 14' W) while the other three had been born in captivity. They were maintained on a diet of frozen herring *Clupea harengus* supplemented with vitamins (Geraci, 1975). During the summer of 1986, seals were typically food deprived one day of the week (usually Sunday). The study was conducted over two consecutive summers.

In 1985 (July 1- Sept 1) a preliminary study of the sleeping patterns of 8 of the harbour seals was undertaken (the 9th seal was born in July, 1986). Individual seals were observed daily, for on average 8 hours, and sleeping bouts were recorded for 10 minute periods by noting the time it took for each animal to begin and end sleep. In addition to sleep time, meteorological conditions, feeding time, and haul-out order were also recorded.

In 1986 (July 27-Oct 25) behavioural observations were carried out on 5 harbour seals. Two of the seals were adult males (ages 16 and 12), one was an adult female (age 11) as well as a juvenile (age 3) and a pup. Three of the seals from the previous year were returned to Miquelon and one died. Seal activity was recorded using a JVC compact video camera (Model# GX-N4UT) connected to a colour video cassette recorder (Model#HR-7200). The camera was mounted on a tripod in an adjacent lab approximately 20 meters from the seal tank, such that the tank was in full frame in the view finder. Security lights over the seal

compound provided sufficient illumination for taping at night. The animals were assumed to be resting on land if they were not present in the tank. Recordings were obtained over a 24 hour period on JVC T-120 video cassettes. From each 24 hours of tape, 48 evenly distributed 5 minute samples were selected for analysis. In order to obtain an indication of how much time seals spend sleeping on land versus in the water, from October 21-25 two cameras were set up to record simultaneously. The cameras were mounted on a metal rod (2" by 30") so that one camera could record activity on land while the other recorded activity in the tank. The tapes for activity in the tank were scored as before, whereas the others were used to record sleep and vigilance on land. In addition to examining sleep patterns on land, sleep location was also noted (ie; whether seals slept on one of two available ramps or in a smaller tank adjacent to the large one).

A grid constructed on a transparency was attached to the screen of a 20" Magnasonic colour television monitor. The grid divided the tank into four equal quadrants and activity was defined by frequency of quadrant entry. Recognition of individual animals on videotape was accomplished through the use of a white oil-based paint rubbed on the animals back. Two of the five seals were marked with different patterns while the other three could be distinguished on the basis of size.

The videotapes were analyzed for the following:

1. Activity - the total number of grid crosses per 5 minute sample period for each seal.
2. Behavioural Categories;
 - a. Flipper slapping- the animal lies on its side and splashes the surface of the water with its foreflipper and/or hindflipper.
 - b. Bubble blowing- the animal emits a stream of bubbles just beneath the water's surface.
 - c. Sleep- Land; the animal remains motionless with eyes closed and neck in a retracted position. When seals sleep on land they typically elevate their heads and scan their surroundings every few minutes or so. Water; the animal's head is tilted backward above the surface of the water and its eyes are closed. Underwater; the animal lies motionless usually at the bottom of the tank.

- d. Aggressive interaction- an encounter between animals where there is biting, lunging, growling or fighting taking place.
- e. Swimming pattern- circuits around the perimeter of the tank in either a clockwise or counterclockwise direction.
- f. In which quadrant of the tank time was spent.

The occurrence, duration and quadrant location of each behaviour was recorded as well as the identity of the seal(s) involved.

A record was also kept of air temperature, cloud cover and amount eaten by each seal.

A total of 28 samples distributed evenly over the observation period was scored by another person to obtain an inter-scorer reliability coefficient.

Chapter 3

RESULTS

The inter-scorer reliability coefficient was 0.90.

3.1. LOCOMOTOR ACTIVITY

Figures 3-(1 to 5) shows the mean daily activity score (expressed as number of grid crosses) for each seal in blocks of seven days over the observation period (July 27 - Oct 25). Over the season, the adults were significantly more active than the younger seals (Table 3-1). The season was divided into four periods; pre-mate (July 27- Aug 4), mate-moult (Aug 5- Aug 18), moult (Aug 19- Sept 12), and post-moult (Sept 13- Oct 25) (Table 3-2). The activity of the adult males declined over the season, male 1, with whom the female mated, becoming quiescent sooner than male 2. The female and younger animals did not alter their activity levels over the season.

Table 3-3 shows the mean daily activity score for each seal collapsed across sample period. A circadian activity rhythm was apparent in all the animals (Figures 3-6 to 3-10) with most activity occurring during the day ($F=14.82$, $df=3,135$ $p=.000$, Table 3-3). Significant differences in activity were found among animals ($F= 6.20$, $df= 4,45$ $p=.000$) and across sample periods ($F= 14.82$, $df=3,135$ $p=.000$). The greatest activity was seen between the hours of 6AM and 6PM for all five seals. Significant pre-post mating differences were also found ($F=56.66$, $df= 1,26$ $p=.000$ Table 3-4). Activity was highest for both males before mating, however their circadian variations in activity was clearest after mating.

Over the period of this study (July 27-Oct25), the average daily intake of food was 3840.58g per seal (Table 3-5). The males ate significantly less food each day

Figure 3-1: Mean daily activity score of male 1 in blocks of 7 days over the observation period.

ACTIVITY OF MALE 1

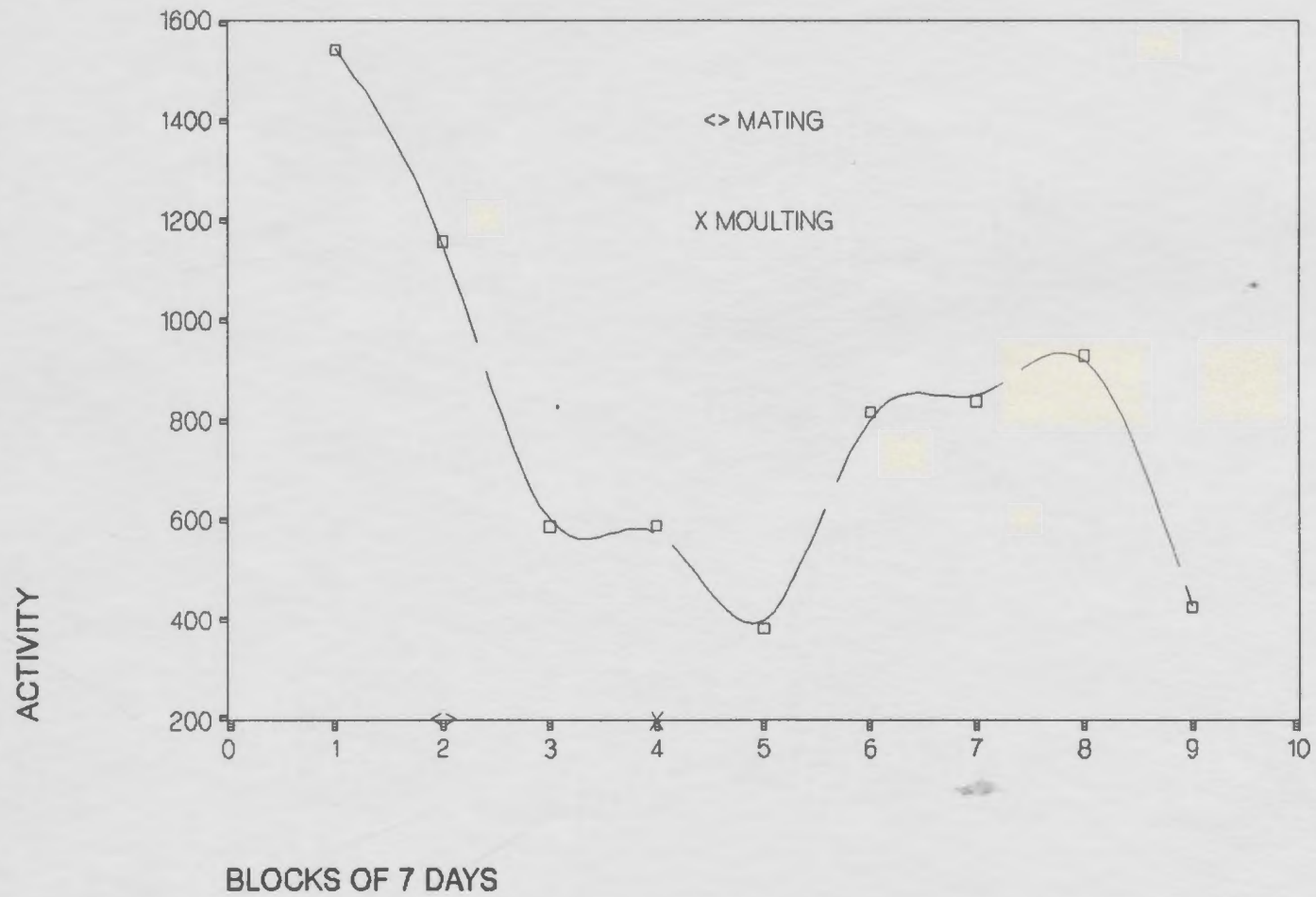
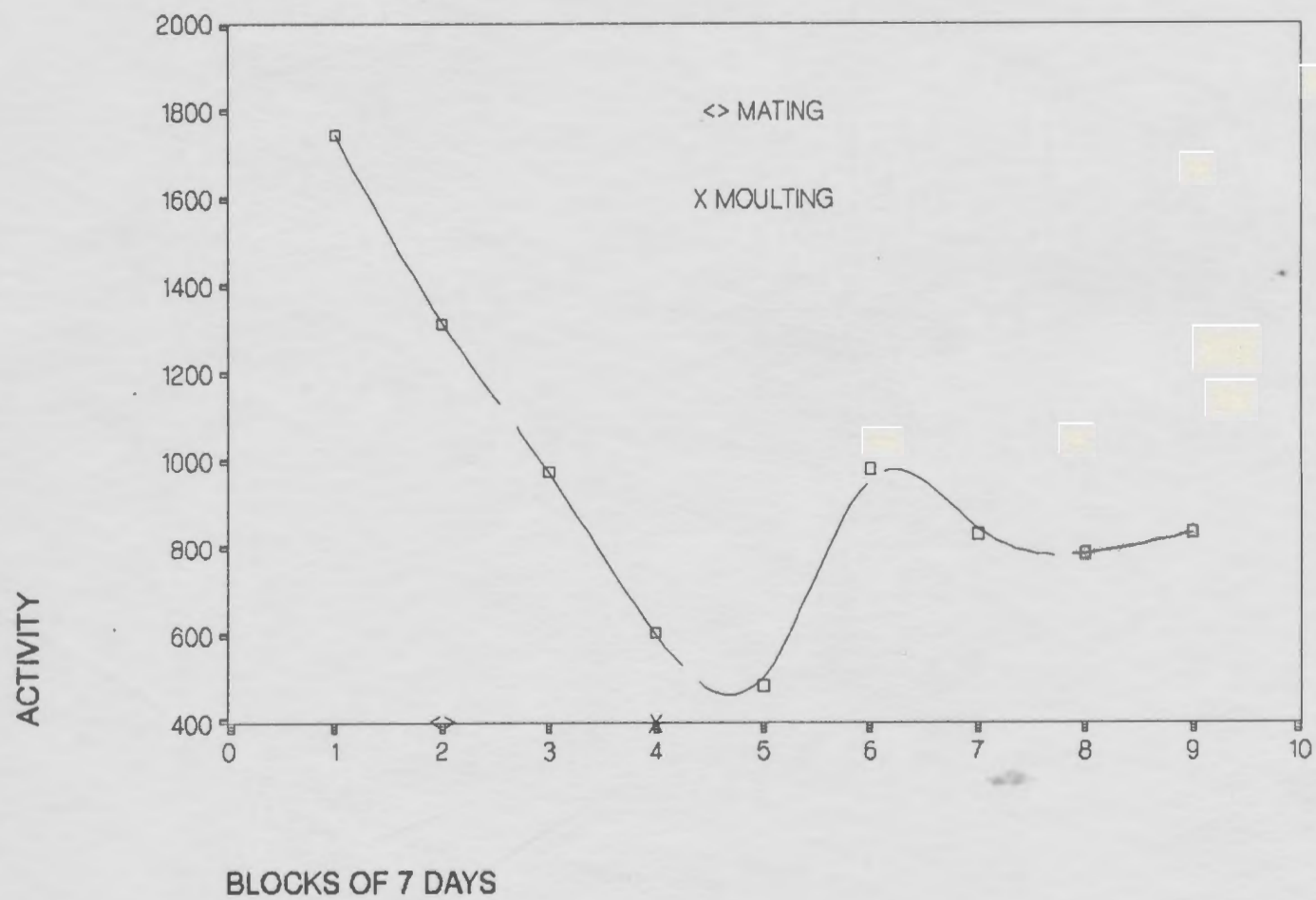


Figure 3-2: Mean daily activity score of male 2 in blocks of 7 days over the observation period.

ACTIVITY OF MALE 2



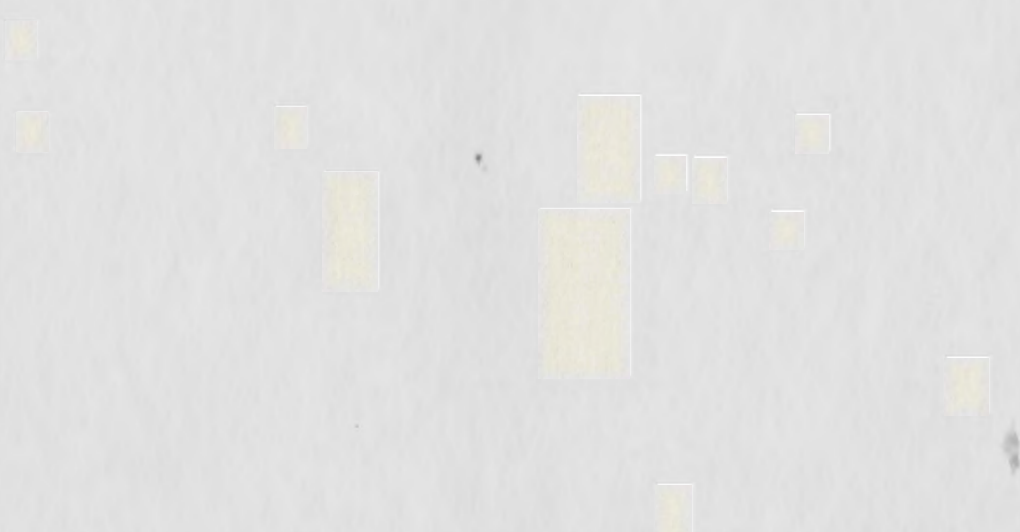


Figure 3-3: Mean daily activity score of female in blocks of 7 days over the observation period.

ACTIVITY OF FEMALE

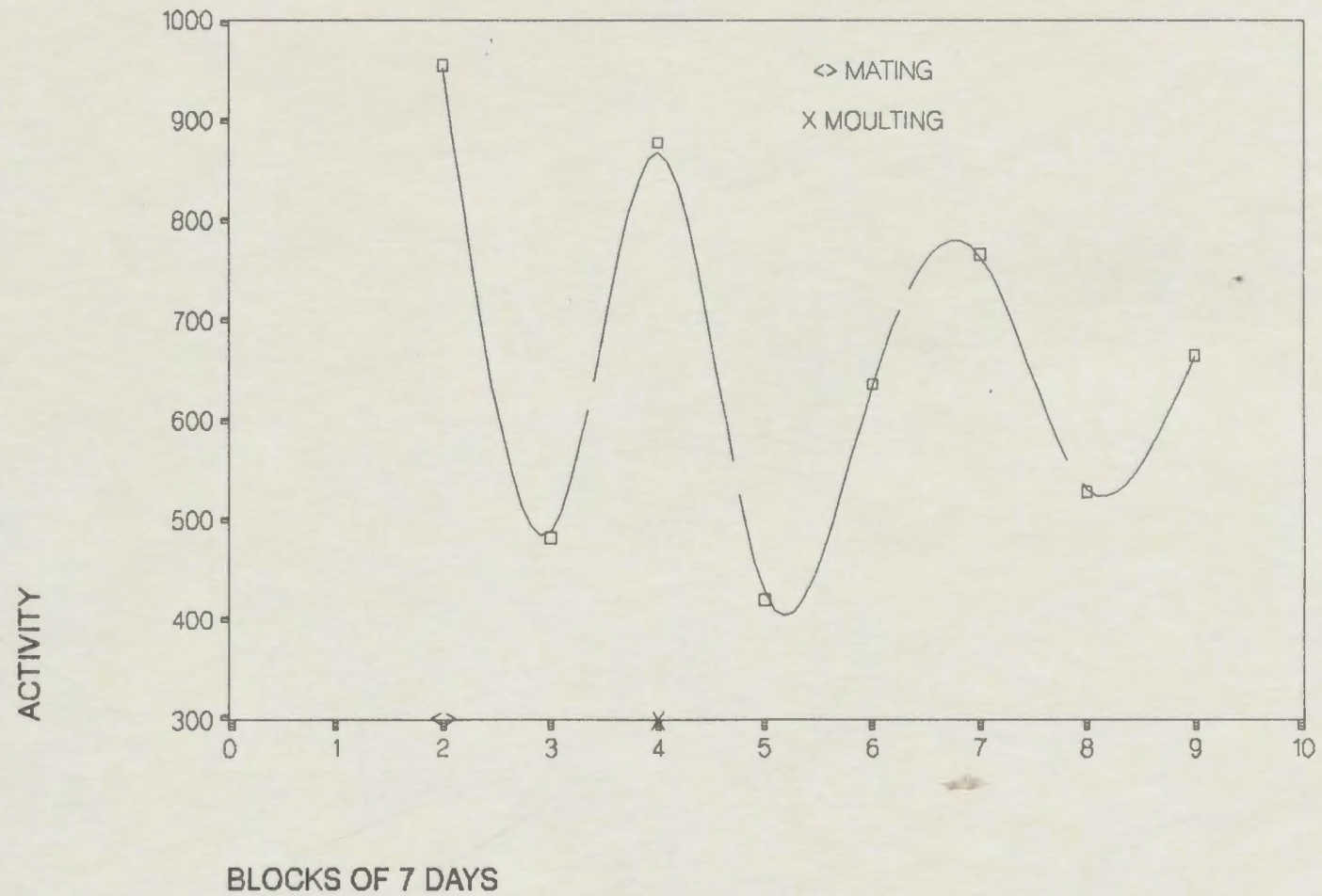
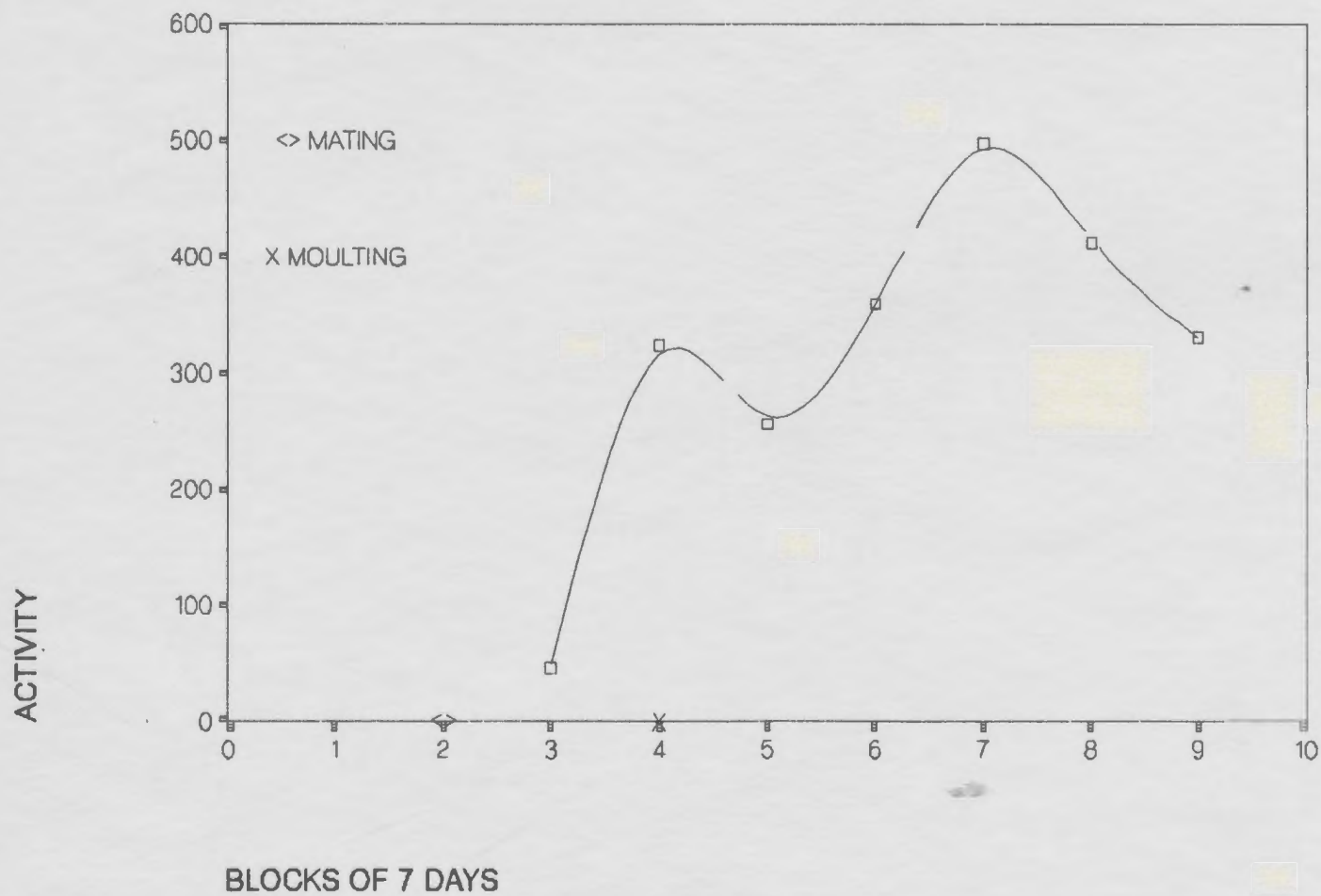


Figure 3-4: Mean daily activity score of pup in blocks of 7 days over the observation period.

ACTIVITY OF PUP






Figure 3-5: Mean daily activity score of juvenile in blocks of 7 days over the observation period.

ACTIVITY OF JUVENILE

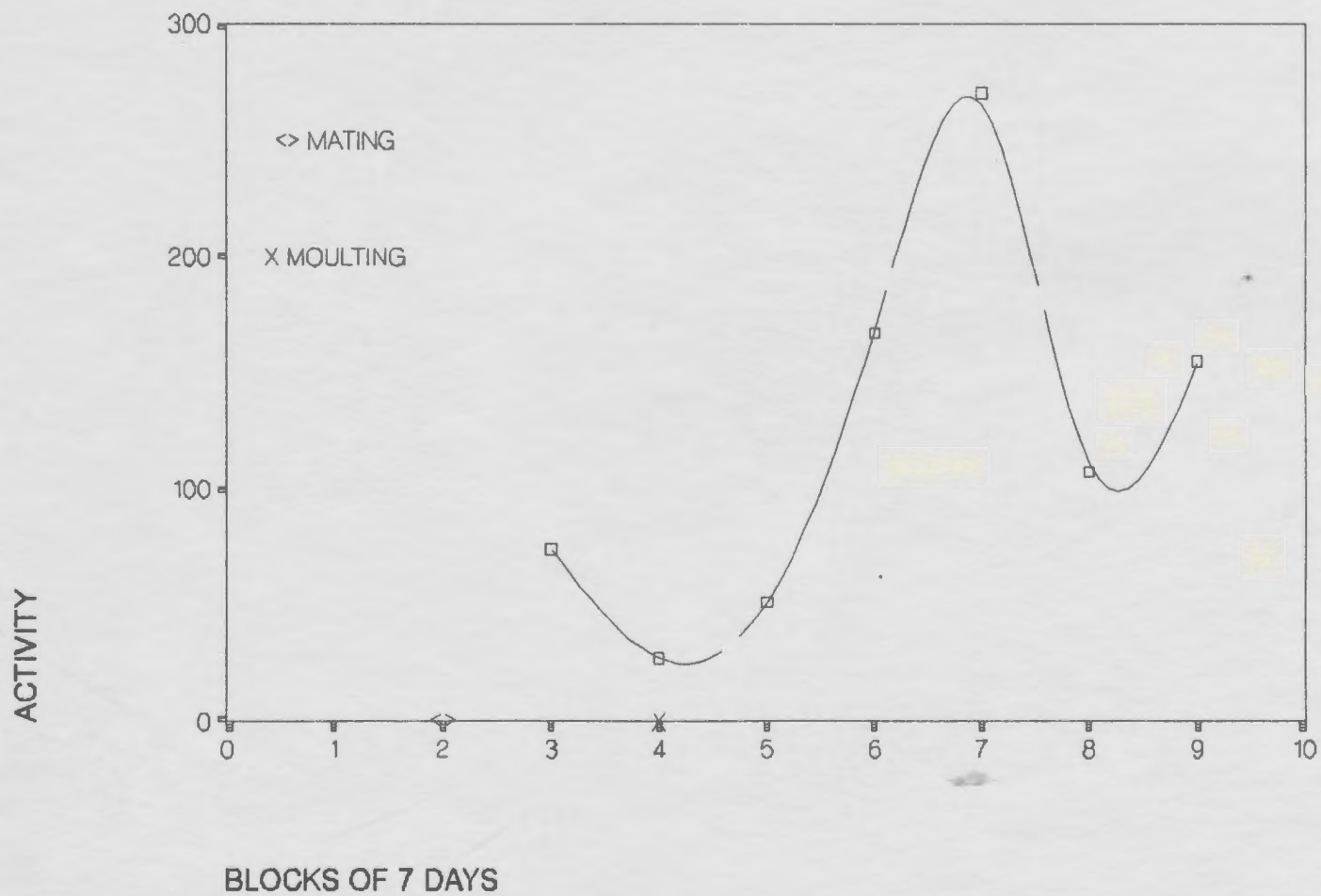


Figure 3-6: Mean daily activity score of male 1 over 24 hours.

ACTIVITY OF MALE 1 OVER 24 HOURS

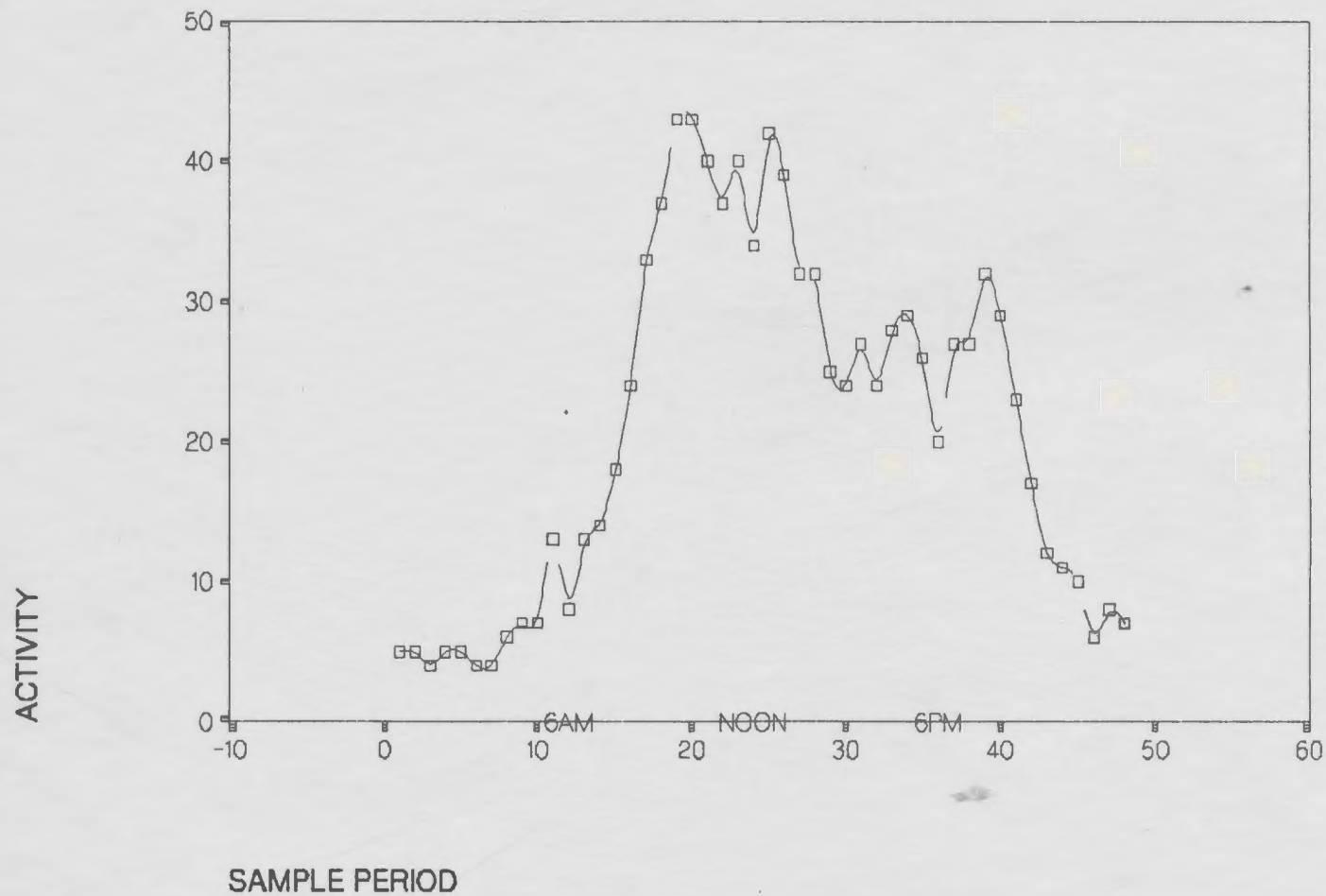


Figure 3-7: Mean daily activity score of male 2 over 24 hours.

ACTIVITY OF MALE 2 OVER 24 HOURS

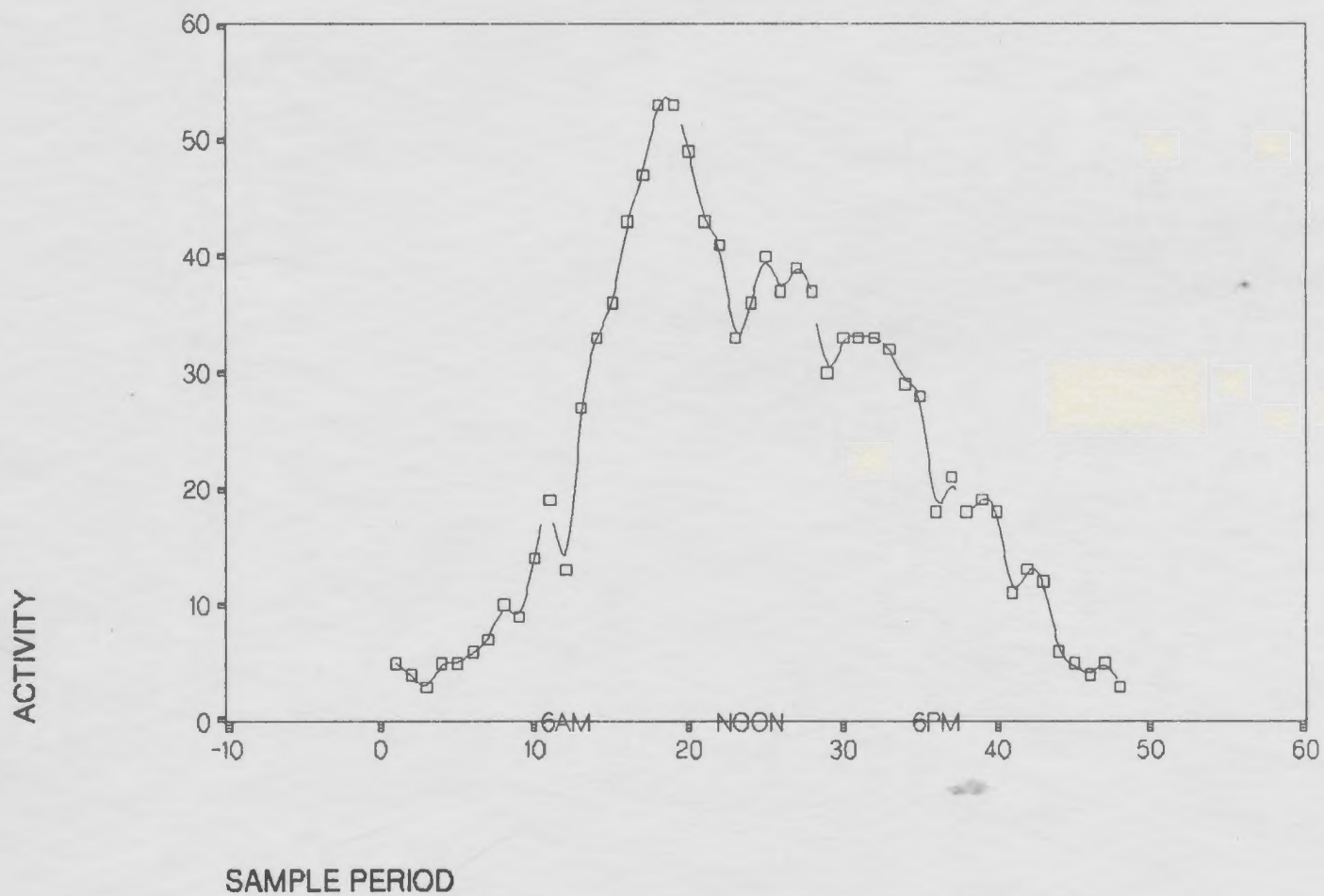


Figure 3-8: Mean daily activity score of female over 24 hours.

ACTIVITY OF FEMALE OVER 24 HOURS

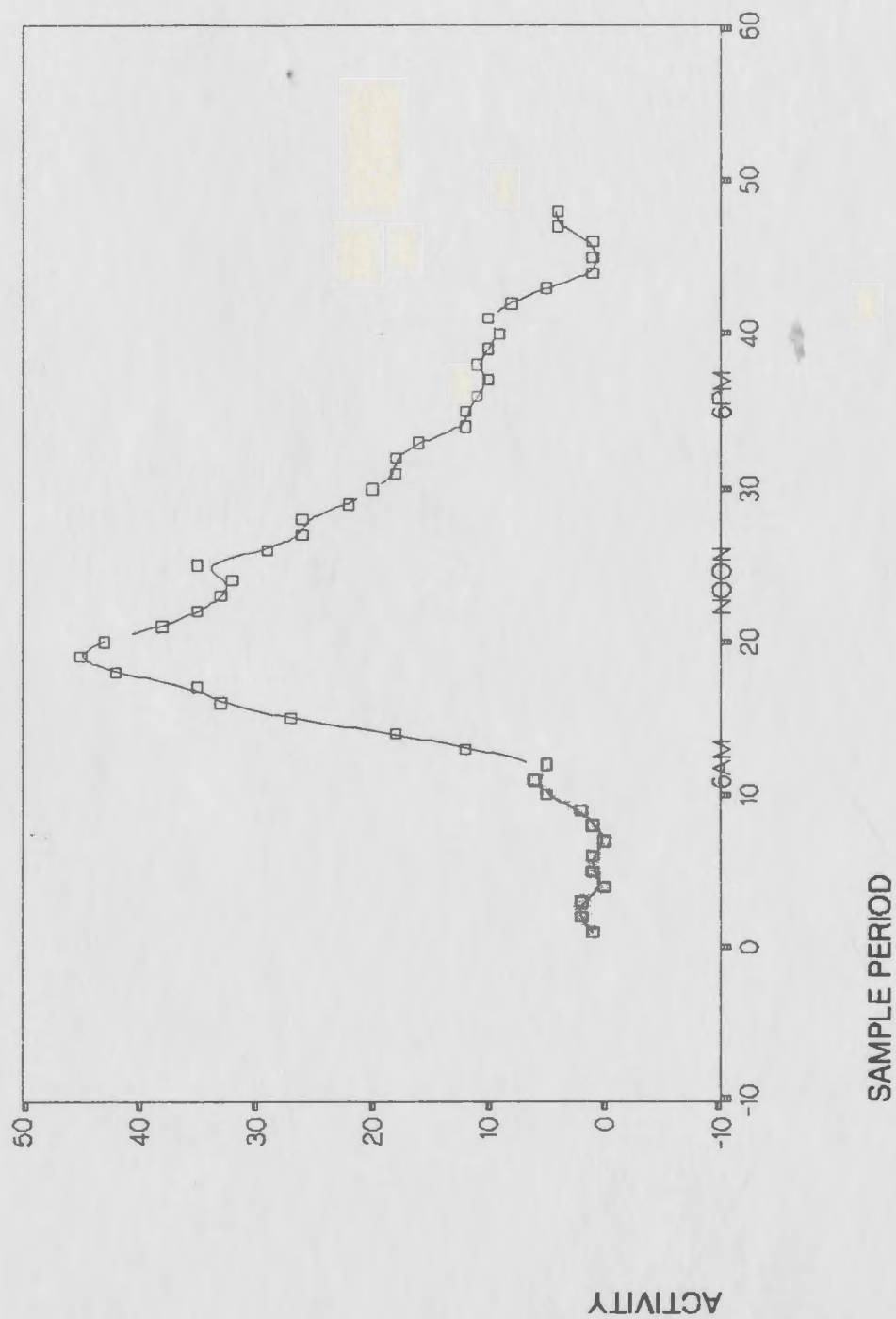
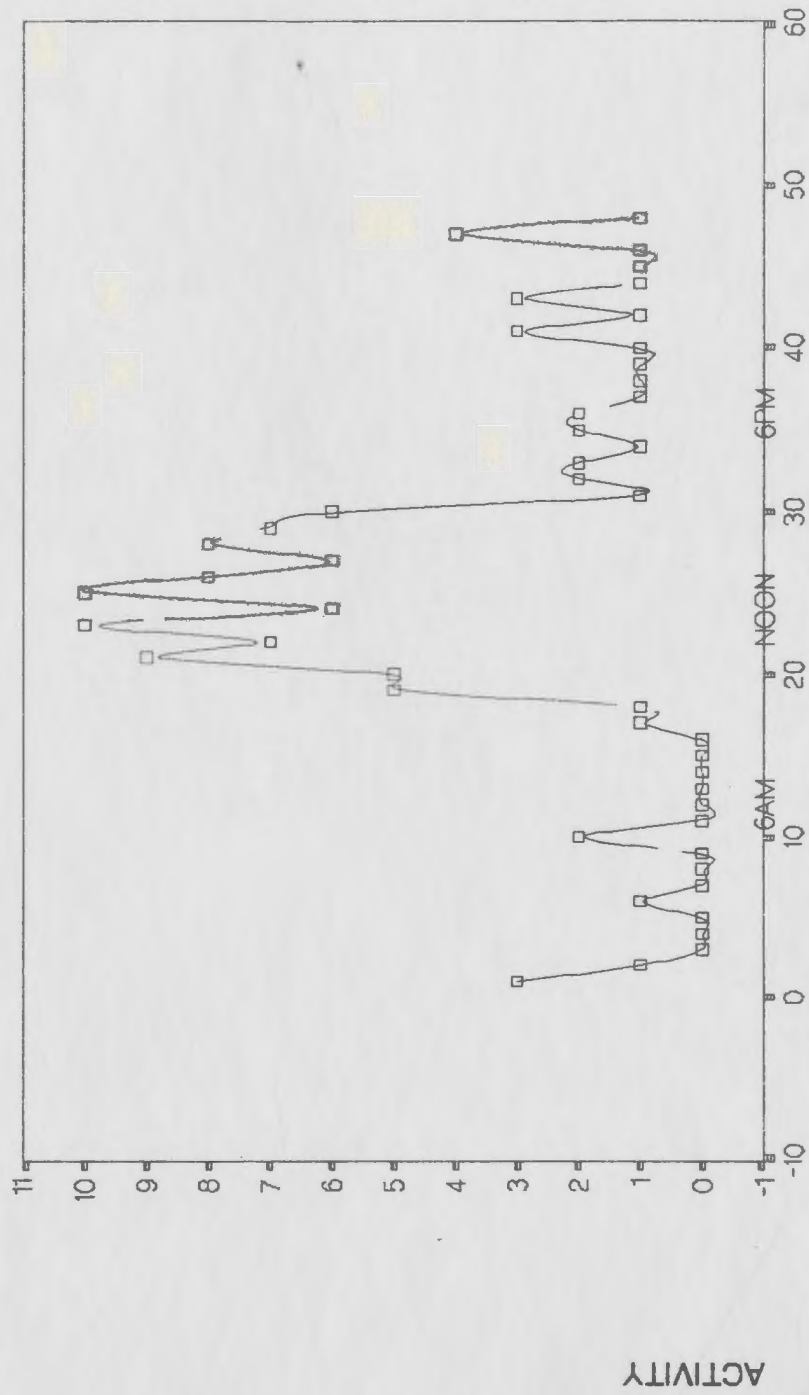


Figure 3-9: Mean daily activity score of pup over 24 hours.

ACTIVITY OF PUP OVER 24 HOURS



SAMPLE PERIOD

Figure 3-10: Mean daily activity score of juvenile over 24 hours.

ACTIVITY OF JUVENILE OVER 24 HOURS

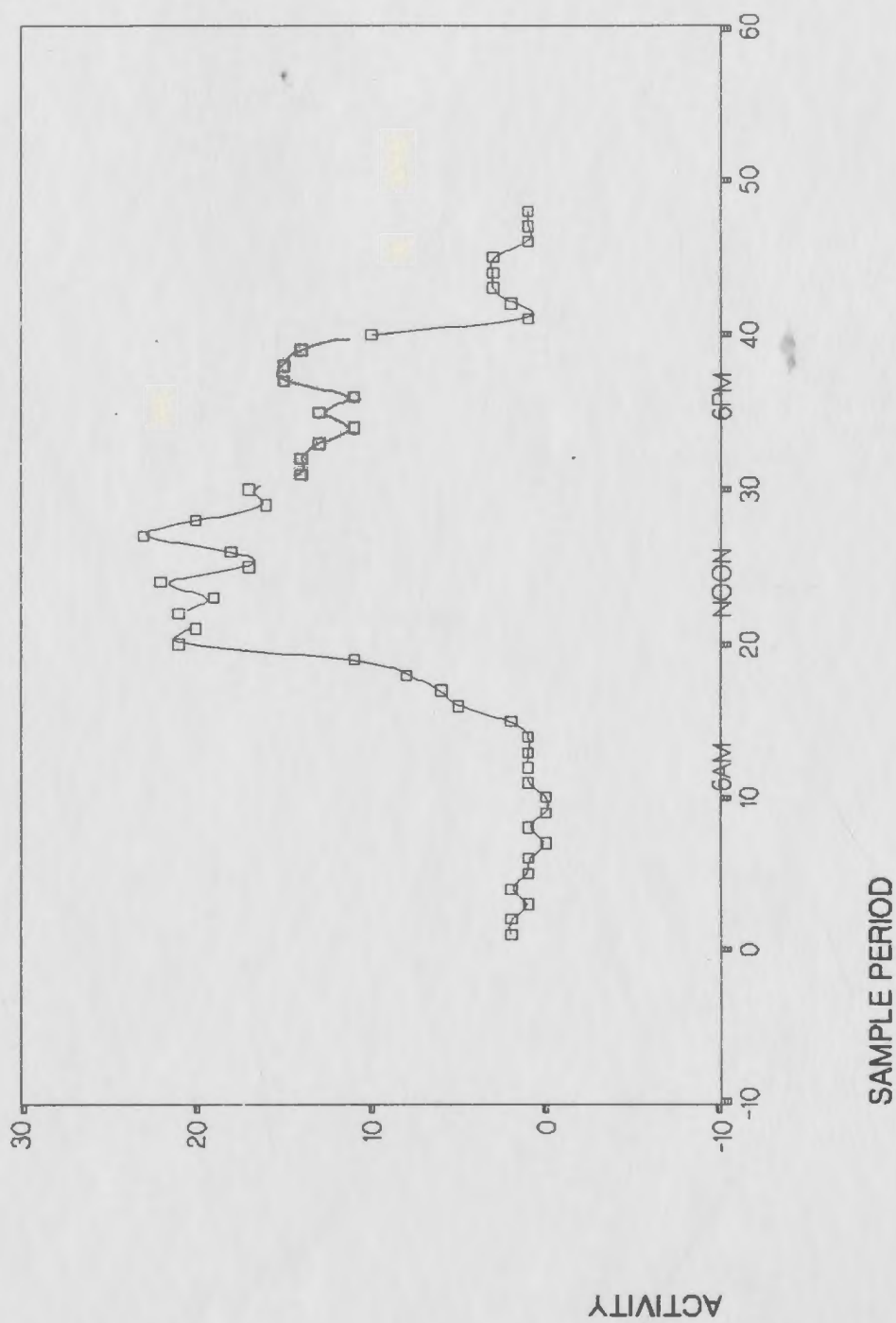


TABLE 3-1:

MEAN DAILY ACTIVITY SCORE OF EACH SEAL FROM JULY
27, 1986 TO OCTOBER 25, 1986.

	MEAN	S
MALE 1	866.81	555.07
MALE 2	966.77	530.88
FEMALE	638.92	273.76
PUP	104.17	86.04
JUVENILE	349.26	182.60

$\bar{X} = 585.19$

F= 22.75 DF 4,215 P=.0000

SCHEFFE: MALE 1 * PUP, JUVENILE

MALE 2 * FEMALE, PUP

JUVENILE

FEMALE * PUP

NOTE: * SIGNIFICANTLY DIFFERENT

TABLE 3-2:

MEAN DAILY ACTIVITY SCORE OF EACH SEAL OVER THE SEASON.

	1	2	3	4
	PRE-MATE	MATE-MOULT	MOULT	POST-MOULT
MALE 1	1467.11	890.23	682.46	785.15
MALE 2	1657.78	1079.21	751.60	781.08
FEMALE	-----	612.6	656.92	624.54
PUP	-----	74.0	69.57	137.78
JUVENILE	-----	331.0	328.37	282.62
\bar{X} =	1562.45	597.41	497.78	538.83

MALE 1	F=	5.62	DF	3,57	P=	.0020	SCHEFFE:	1*3,4
MALE 2	F=	10.67	DF	3,57	P=	.0000	SCHEFFE:	1*3 4*2
FEMALE	F=	0.1137	DF	2,45	P=	.8928	SCHEFFE:	NS
PUP	F=	1.45	DF	2,15	P=	.2661	SCHEFFE:	NS
JUVENILE	F=	0.3371	DF	2,31	P=	.7164	SCHEFFE:	NS

NOTE: * SIGNIFICANTLY
DIFFERENT

TABLE 3-3:

MEAN DAILY ACTIVITY SCORE OF EACH SEAL OVER 24 HOUR
SAMPLE PERIOD.

	1	2	3	4	
	12-6AM	6AM-12	12-6PM	6PM-12	
MALE 1	113.7	458.2	358.7	191.1	
MALE 2	96.5	371.8	415.3	354.5	
FEMALE	24.9	109.5	221.5	95.1	
PUP	22.3	210.3	268.3	101.7	
JUVENILE	12.8	63.2	121.6	88.6	

SOURCE	SS	DF	MS	F	P
BETWEEN-SUBJECT					
SEAL	1750470.15	4	435117.54	6.20	.000
WITHIN	3174828.33	45	70551.74		
WITHIN-SUBJECT					
SAMPLE PERIOD	976673.32	3	325557.77	14.82	.000
WITHIN	2966453.37	135	21973.73		
INTERACTIONS					
SEAL BY SAMPLE PERIOD	587134.15	12	48927.85	2.23	.014

TABLE 3-4:

MEAN DAILY ACTIVITY SCORE OF EACH SEAL OVER 24 HOUR
SAMPLE PERIOD BEFORE AND AFTER MATING.

		1	2	3	4
		12-6AM	6AM-12	12-6PM	6PM-12
MALE 1	PRE	305.40	774.20	386.80	455.60
	POST	39.60	215.90	352.50	98.30
MALE 2	PRE	241.80	509.00	518.80	563.80
	POST	17.90	225.00	389.10	329.30

NOTE* THE OTHER THREE SEALS WERE NOT INCLUDED IN THE
ANALYSIS SINCE THEY WERE NOT IN THE TANK PRE-MATE.

SOURCE	SS	DF	MS	F	P
BETWEEN-SUBJECT					
PRE-POST	1816212.02	1	1816212.0	56.66	.000
SEAL	11537.07	1	11537.07	0.36	.554
PRE-POST BY SEAL	49192.07	1	49192.07	1.53	.226
WITHIN	833350.35	26	32051.94		
WITHIN-SUBJECT					
SAMPLE PERIOD	1321712.48	3	440570.83	14.31	.000
WITHIN	2401541.85	78	30789.00		
INTERACTIONS					
PRE-POST	394452.35	3	131484.12	4.27	.008
BY SAMPLE PERIOD					
SEAL	349039.43	3	116346.48	3.78	.014
BY SAMPLE PERIOD					
PRE-POST	119436.43	3	39812.14	1.29	.283
BY SEAL BY SAMPLE PERIOD					

TABLE 3-5:

AVERAGE DAILY FOOD INTAKE (IN GRAMS) OF EACH SEAL FROM
JULY 27, 1986 TO OCTOBER 25, 1986.

	MEAN	S
MALE 1	4159.63	1343 53
MALE 2	3932.45	1201.49
FEMALE	4114.19	1057.92
PUP	3455.56	806.40
JUVENILE	3541.07	1028.67
	$\bar{X} = 3840.58$	

F= 1.89 DF 4,182 P=.1145

SCHEFFE: NO TWO GROUPS ARE
SIGNIFICANTLY DIFFERENT

TABLE 3-6:

AVERAGE DAILY FOOD INTAKE OF EACH SEAL OVER THE
SEASON (July 27, 1986 to October 25, 1986).

	1	2	3	4
	PRE-MATE	MATE-MOULT	MOULT	POST-MOULT
MALE 1	2073.75g	3461.67g	4552.08g	4560.00g
MALE 2	2923.75g	3570.83g	4895.20g	4000.00g
FEMALE	-----	3366.67g	4352.80g	4198.89g
PUP	-----	-----	4433.33g	2966.67g
JUVENILE	-----	2200.00g	3772.22g	3227.78g
	X= 2498.75g	3149.79g	4401.13g	3790.67g
MALE 1	F= 13.84 DF 3,49 P=.0000 SCHEFFE: 2*1 3*1,2 4*1			
MALE 2	F= 10.83 DF 3,50 P=.0000 SCHEFFE: 3*1,2			
FEMALE	F= 3.22 DF 2,40 P=.0505 SCHEFFE: NS			
PUP	F= 33.46 DF 1,7 P=.0007 SCHEFFE: NS			
JUVENILE	F= 1.83 DF 2,25 P=.1817 SCHEFFE: NS			

NOTE: * SIGNIFICANTLY
DIFFERENT

TABLE 3-7:

MEAN DAILY ACTIVITY SCORES FOR EACH SEAL AS A FUNCTION OF EATING (1) $< OR = .50$ AVERAGE DAILY MEAL (2) $> .50$ AND $< OR =$ AVERAGE DAILY MEAL (3) $>$ AVERAGE DAILY MEAL AND $< OR =$ 1.50 AVERAGE DAILY MEAL, OR (4) > 1.50 AVERAGE DAILY MEAL.

	1	2	3	4
MALE 1	2077.00	1138.16	545.91	791.83
MALE 2	2054.00	1299.47	841.91	657.00
FEMALE	1018.00	604.71	664.13	560.31
PUP	-----	356.20	301.27	391.60
JUVENILE	-----	121.00	92.80	97.17

MALE 1: F= 7.90 df=3,50 p=.0002 SCHEFFE 3*2,1
 MALE 2: F= 8.19 df=3,52 p=.0001 SCHEFFE 4*2,1: 3*2
 FEMALE: F= 1.05 df=3,40 p=.3813
 PUP: F= 0.78 df=2,27 p=.4701
 JUVENILE: F= 0.08 df=2,15 p=.9264

NOTE * SIGNIFICANTLY
DIFFERENT

before mating than after. The female and young animals did not alter the amount they ate over the season (Table 3-6). On days the group was eating less than the mean, both adult males were significantly more active; when they consumed more than the average, their general locomotion was reduced. The female's activity level remained roughly constant regardless of the amount she ate (Table 3-7), as did that of the pup and juvenile.

3.1.1. Time Series Analyses

A Box-Jenkins Interrupted Time Series Analysis was used to look at pre-post mate and moult changes in activity. A Time Series Analysis typically consists of 3 stages; identification of an appropriate model, estimation, and testing the adequacy of fit (Cook & Campbell, 1979). The first step, identification is accomplished by both plotting the data and examining the autocorrelations (ACF) and partial autocorrelations (PACF) between adjacent data points. After doing this, the data are fitted to an appropriate model. The ACF and PACF are used in identifying the appropriate model. There are two models frequently encountered in a time series analysis: the autoregressive and moving average. The ACF provides useful information for determining autoregressive polynomials and the PACF for moving average polynomials. Each model has a theoretical ACF and PACF associated with it. The estimated ACF'S and PACF's are compared to the theoretical ones and a model is chosen based on similarities. Once a model has been chosen, the next step involves estimating the parameters alpha and beta. The ACF and PACF are computed from residuals of the estimated tentative model and these statistics are used to decide whether the model chosen is the appropriate one. If the estimated coefficients do not satisfy certain mathematical conditions, the model chosen is rejected and a different one is tried. When a suitable model is found, the next step involves introducing the intervention, which in this case is the occurrence of mating and moulting. The appropriate model for this analysis was the autoregressive one. It was discovered upon examination of the data that a 7 day cycle was present; that is, something took place every seven days that resulted in an increase in activity levels. Although a seven day cycle was

found, the occurrence of mating and moulting did not affect activity levels of the adult males. Parameter values were found to be $\alpha_1 = .4632$ and $\alpha_2 = .4360$ which are statistically insignificant.

3.2. SOCIAL INTERACTION

3.2.1. Copulation

Copulation occurred three times on August 5 between male 1 and the female. Male 2 made several attempts but was unsuccessful. On one occasion male 2 was in the tank with the female. Male 1 entered the tank, lunged toward male 2 and chased him out of the water (aside from this single incident, agonistic encounters never occurred during any sample period). Prior to male 1's entry the female appeared receptive to male 2. She swam close to him around the perimeter of the tank. He attempted to mate with her while male 1 was in the water but quickly retreated after the attack by male 1. On the other two occasions male 1 was alone with the female in the tank. Male 1 mounted the female at the surface of the water and the two sank. After a few minutes they came up to the surface briefly and then sank again. Male 1 was lying on the female's back with his hindflippers curled around her's, after which penile insertion took place. He made several thrusting movements with his lower abdomen and the two animals came up to the surface, disengaged and swam around the perimeter of the tank.

3.2.2. Displays

The two mature males engaged in flipperslapping and bubbleblowing. The juvenile, pup and female never did so. Tables 3-8 and 3-9 show the frequency and mean duration of each behaviour by month. The majority of displays were seen during July and August, just prior to copulation. The only displays seen after mating were by male 2. Male 2 flipperslapped on 14 occasions after mating occurred and bubbleblew 52 times. The longest displays during the month of July were seen by male 1 (Table 3-8 and 3-9). Significant pre-post mate differences were seen between animals with respect to flipperslapping ($F = 29.57$ df 4,213

$p=.000$) and bubbleblowing ($F=10.81$ df 4,213 $p=.000$) (Table 3-10 and 3-11). Male 1 displayed in all four quadrants before mating. The majority of displays occurred in quadrant 2 (Table 3-10 and 3-11). Male 2 flipperslapped in quadrant 4 prior to mating but after mating he displayed in quadrants 1,2, and 4. He bubbleblew in quadrants 2,3, and 4 pre-mate but post-mate he displayed in quadrants 1,2, and 4. Male 1 swam counterclockwise 70% of the time while male 2 swam clockwise 95% of the time (Table 3-12).

3.3. SLEEP

The two adult males did not sleep during any of the 5 minute samples analyzed for the 7 days preceding copulation. Table 3-13 shows the mean sleep duration in the water for the individual seals. No significant differences were found among the animals overall. During the month of August, each seal slept an average of 59.88 s during the samples each day. This increased to 923.05 s during the month of September and to 1795.88 s in Oct (Table 3-14). Pearson correlation coefficients of activity with sleep and sleep with food total for each animal showed no significant results. Table 3-15 shows the mean daily sleep duration on land of each seal. Significant differences were seen between individual animals with respect to sleep on land ($F=103.86$ df 4,737 $p=.000$). The juvenile slept the most (264.63s) while the female slept the least (59.03s). Preliminary results from the summer of 1985 (July 1 to September 1) revealed that although these seals sleep both on land and in the water, 86% of their sleep occurred on land versus 14% in the water. It was not possible to ascertain what percentage of time was spent in REM sleep. In 1986, significant differences were seen with respect to sleep location (Table 3-16) only for male 1 who spent most of the time sleeping in the small tank ($F=4.66$ df 4,213 $p=.000$). Significant pre-post mate differences were seen among animals ($F=6.05$ df=12,213 $p=.0000$) (Table 3-17). All five animals were not observed sleeping prior to mating. After mating, male 1 and the juvenile slept in quadrant 2 most of the time while male 2 and the female spent most of the time sleeping in quadrant 3 and the pup slept in quadrant 4.

Scanning occurred only when the seals were hauled out. Table 3-18 shows the

TABLE 3-10:

MEAN DAILY FLIPPERSLAPPING OCCURRENCE AND DURATION (IN SECONDS)
OF EACH SEAL IN DIFFERENT QUADRANTS BEFORE AND AFTER MATING.

		Q1		Q2		Q3		Q4	
		OCC	DUR	OCC	DUR	OCC	DUR	OCC	DUR
MALE 1	PRE	3.00	20.41	54.17	493.50	.17	.92	.17	1.42
	POST	0	0	0	0	0	0	0	0
MALE 2	PRE	0	0	0	0	0	0	1.90	19.10
	POST	.078	.588	.020	.059	0	0	.020	.353

SOURCE	SS	DF	MS	F	P
BETWEEN-SUBJECT					
PRE-POST	263.62	1	263.62	7.65	.006
SEAL	4073.30	4	1018.33	29.57	.000
PRE-POST BY SEAL	4098.27	4	1024.58	29.75	.000
WITHIN	7335.30	213	34.44		
WITHIN-SUBJECT					
QUADRANT	619.41	3	206.47	6.86	.000
WITHIN	19228.25	639	30.09		
INTERACTIONS					
PRE-POST	619.91	3	206.64	6.87	.000
BY QUADRANT					
SEAL	11214.70	12	934.56	31.06	.000
BY QUADRANT					
PRE-POST	11209.05	12	934.09	31.04	.000
BY SEAL BY QUADRANT					

TABLE 3-11:

MEAN DAILY BUBBLEBLOWING OCCURRENCE AND DURATION (IN SECONDS)
OF EACH SEAL IN DIFFERENT QUADRANTS BEFORE AND AFTER MATING.

		Q1		Q2		Q3		Q4	
		OCC	DUR	OCC	DUR	OCC	DUR	OCC	DUR
MALE 1	PRE	1.25	7.33	28.25	214.92	1.17	6.25	.417	2.25
	POST	0	0	0	0	0	0	0	0
MALE 2	PRE	0	0	.500	4.30	.100	.600	12.50	102.30
	POST	.039	.255	.137	1.49	0	0	.020	1.02
SOURCE		SS		DF	MS	F		P	
BETWEEN-SUBJECT									
PRE-POST		145.14		1	145.14	9.24	.003		
SEAL		678.86		4	169.72	10.81	.000		
PRE-POST BY SEAL		689.49		4	172.37	10.97	.000		
WITHIN		3345.46		213	15.71				
WITHIN-SUBJECT									
QUADRANT		153.83		3	51.28	3.89	.009		
WITHIN		8432.46		639					
INTERACTIONS									
PRE-POST		151.33		3	50.44	3.82	.010		
BY QUADRANT									
SEAL		4088.98		12	340.75	25.82	.000		
BY QUADRANT									
PRE-POST		4132.76		12	344.40	26.10	.000		
BY SEAL BY QUADRANT									

TABLE 3-12:

MEAN DAILY SWIMMING DIRECTIONS OF MALE SEALS.

	CLOCKWISE	COUNTERCLOCKWISE
MALE 1	5.80	14.35
MALE 2	21.17	1.15

F (SEAL)= 164.61 DF 4,8839 P=.000

F (SWIM DIRECTION)= 238.99 DF 1,8839 P=.000

TABLE 3-13:

MEAN DAILY SLEEP DURATION IN WATER (IN SECONDS) OF
INDIVIDUAL SEALS FROM JULY 27, 1986 TO OCTOBER 25, 1986.

	MEAN	S
MALE 1	412.00	858.02
MALE 2	820.72	1564.40
FEMALE	463.40	1101.46
PUP	33.17	102.62
JUVENILE	840.82	1834.72
	$\bar{X} = 514.02$	

F= 2.03 DF 4,215 P=.0909

TABLE 3-14:

MEAN DAILY SLEEP DURATION IN WATER (IN SECONDS) OF
INDIVIDUAL SEALS BY MONTH.

	JULY	AUG	SEPT	OCT
MALE 1	0	81.14	1034.50	253.00
MALE 2	0	110.29	1457.95	3497.20
FEMALE	----	74.22	886.40	561.60
PUP	----	32.83	-----	80.00
JUVENILE	----	0.91	313.33	4587.60

\bar{X} = ---- 59.88 923.05 1795.88

NOTE: THE FEMALE, PUP, AND JUVENILE WERE NOT OBSERVED
IN THE TANK IN JULY. THE PUP WAS NOT OBSERVED IN
THE TANK IN SEPTEMBER.

MALE 1	F= 7.08	DF 3,55	P=.0004	SCHEFFE: 3*2
MALE 2	F= 14.26	DF 3,57	P=.0000	SCHEFFE: 3*2 4* 1,2,3
FEMALE	F= 3.21	DF 2,45	P=.0500	SCHEFFE: NS
PUP	F= 0.87	DF 2,15	P=.4378	SCHEFFE: NS
JUVENILE	F= 45.72	DF 2,31	P=.0000	SCHEFFE: 4*2,3

number of scanning occurrences per seal. A chi-square test revealed significant differences between seals ($p < 0.001$). The juvenile scanned the most whereas the pup scanned the least. Table 3-19 shows the mean daily scanning durations of individual seals, and no significant difference was found among animals. When sleep occurred in the water during a sample, it typically occurred for the entire sample, therefore waking rates in water could not be compared with scanning rates on land.

TABLE 3-15:

MEAN DAILY SLEEP DURATION ON LAND (IN SECONDS) OF
INDIVIDUAL SEALS FROM OCTOBER 21-25, 1986.

	MEAN	S
MALE 1	153.58	107.44
MALE 2	205.46	118.04
FEMALE	59.03	46.41
PUP	76.59	77.31
JUVENILE	264.63	81.35
<hr/>		
	$\bar{X} = 151.86$	

F= 103.86 DF 4,737 P=.0000 SCHEFFE: MALE 1* FEMALE,
PUP

MALE 2* MALE 1
FEMALE, PUP
JUVENILE* MALE 1
MALE 2, FEMALE,
PUP

NOTE: * SIGNIFICANTLY
DIFFERENT

TABLE 3-16:

MEAN DAILY SLEEP DURATION (IN SECONDS) OF EACH SEAL AS A
FUNCTION OF LOCATION FROM OCTOBER 21-25, 1986.

	BIG RAMP	SMALL RAMP	SMALL TANK
MALE 1	144.87	45.50	297.69
MALE 2	110.69	120.19	28.50
FEMALE	73.81	28.60	-----
PUP	-----	64.48	103.70
JUVENILE	42.50	-----	-----

MALE 1	F= 26.76	DF 2,286	P=.0000	SCHEFFE: 3*1,2
MALE 2	F= .68	DF 2,75	P=.5115	SCHEFFE: NS
FEMALE	F= 1.57	DF 1,66	P=.2141	
PUP	F= 50.45	DF 1,370	P=.0000	

NOTE: * SIGNIFICANTLY
DIFFERENT

TABLE 3-17:

MEAN DAILY SLEEP OCCURRENCE AND DURATION OF EACH SEAL
BEFORE AND AFTER MATING.

		Q1		Q2		Q3		Q4	
		OCC	DUR	OCC	DUR	OCC	DUR	OCC	DUR
PRE		0	0	0	0	0	0	0	0
MALE 1									
POST		.245	11.63	1.88	335.80	.531	58.45	.571	65.71
PRE		0	0	0	0	0	0	0	0
MALE 2									
POST		.039	10.59	1.43	380.69	1.57	419.47	.745	64.32
PRE		0	0	0	0	0	0	0	0
FEMALE									
POST		.021	.745	.064	19.15	2.32	394.36	.830	39.30
PRE		0	0	0	0	0	0	0	0
PUP									
POST		0	0	0	0	.235	4.41	.412	30.71
PRE		0	0	0	0	0	0	0	0
JUVENILE									
POST		.147	44.12	2.24	618.18	.029	.294	.059	3.24

TABLE 3-17: (continued)

MEAN DAILY SLEEP OCCURRENCE AND DURATION OF EACH SEAL
BEFORE AND AFTER MATING.

SOURCE	SS	DF	MS	F	P
BETWEEN-SUBJECT					
PRE-POST	50.60	1	50.60	6.83	.010
SEAL	138.23	4	34.56	4.66	.001
PRE-POST BY SEAL	148.18	4	37.05	5.00	.001
WITHIN	1578.65	213	7.41		
WITHIN-SUBJECT					
QUADRANT	165.21	3	55.07	9.66	.000
WITHIN	3642.22	639	5.70		
INTERACTIONS					
PRE-POST	78.51	3	26.17	4.59	.003
BY QUADRANT					
SEAL	595.53	12	49.63	8.71	.000
BY QUADRANT					
PRE-POST	413.67	12	34.47	6.05	.000
BY SEAL BY QUADRANT					

TABLE 3-18:

TOTAL SCANNING OCCURRENCES OF INDIVIDUAL SEALS
FROM OCTOBER 21-25, 1986.

MALE 1	26
MALE 2	92
FEMALE	31
PUP	2
JUVENILE	125

2

 $X = 187.67$ $P < 0.001$

TABLE 3-19:

MEAN DAILY SCANNING DURATIONS (IN SECONDS) OF
INDIVIDUAL SEALS FROM OCTOBER 21-25, 1986.

	MEAN	S
MALE 1	11.80	13.53
MALE 2	10.89	7.77
FEMALE	11.52	15.91
PUP	10.40	10.38
JUVENILE	15.00	7.07
	$\bar{X} = 11.92$	

F= .2488 DF 4,271 P=.9102

Chapter 4

DISCUSSION

4.1. LOCOMOTOR ACTIVITY

Overall, the two adult males were more active than the other three animals (Table 3-2). Activity for both males was highest prior to copulation. Boness (1984) reported an increase in activity in adult male elephant seals just before copulation, with the most active males achieving the greatest copulatory success. Male 1's activity score fell abruptly after copulation whereas male 2, who was not observed mating with the female showed a gradual decrease in activity over the season. The female and younger animals did not alter their activity over the season. Both adult males engaged in frequent flipperslapping and bubbleblowing prior to mating and slept little if at all. Their decrease in activity after this time may have been due to the fact that they were spending more time resting during this period to make up for their losses.

The amount of food consumed by the seals varied over the observation period (Table 3-6). Food intake was low just prior to mating but increased thereafter. When food intake was reduced, overall activity of the adult males increased. This inverse relationship between feeding and activity is a common finding, and in some species (Milner, 1970), it is assumed that increased locomotion functions to enhance the probability that the hungry animal will find food. The seals in this study were not deprived, but rather voluntarily reduced the amount they ate. Feeding should not interfere with the displaying of captive animals which do not have to forage. If in the wild, feeding interferes with reproductive displays, it might be that the captive seals are governed by the same "species program". The two adult males in the present study ate less during the weeks prior to mating

when they spent a large proportion of their time engaging in flipperslapping and bubble blowing; after mating, these behaviours rarely occurred. Since the captive animals did not have to spend time foraging, it is not clear why they did not eat more to compensate for the energy needed for frequent displaying. In any event, it seems likely that they increased their food intake and decreased activity after mating to make up for energetic losses.

In the wild, seals show a reduction in food intake during the moult period. This may occur because they spend a large proportion of their time hauled out, which is thought to facilitate the moult process by heightening epidermal mitosis and by raising tissue temperature (Ling, 1974). The animals in the present study showed an increase in food intake during this period perhaps suggesting that seals in the wild would feed more if they were not spending most of the time ashore. The fact that an increase is also seen during the post-moult period (Table 3-6) suggests that these animals may be eating more because they anticipate changes in food availability. This period is a time when local fish numbers such as herring and mackerel are at their lowest, hence their changes in appetite may reflect a "species mechanism". However, this seems unlikely since the female and younger animals did not alter their appetite and activity levels over the season, it seems more likely that the adult males had expended a lot of energy prior to mating and had to compensate for this by lowering activity levels and increasing food intake.

A Time Series Analysis showed that the occurrence of mating and moulting did not significantly affect activity levels in the adult males. It did however, reveal that a seven day cycle was present. Some extraneous environmental event influenced the animal's behaviour every seven days. This group was usually food deprived one day of the week, typically Sunday's which may have been responsible for an increase in activity every seven days.

This is the first description of a circadian rhythm in a Phocid. Hui (1979) reported the presence of a circadian rhythm in the dolphin *Delphinus delphis* with most activity occurring during the day. All five animals in the present study showed an increase in activity between the hours of 6AM-6PM (Table 3-3), suggesting they are diurnal at least in captivity. Tester (1987) looked at activity rhythms of a number of mammals both in the wild and in captivity. He found

that animals in the wild showed much variation in the times when activity began and ended, however animals in captivity showed remarkably precise timing from day to day with respect to onset and termination of activity. Variations in activity and in the amount of rest during the normal active period were shown to be related to changes in such factors as temperature, food supply and breeding behaviour (Tester, 1987). In the present study, the timing of the active period may be altered since wild harbour seals usually feed at night (Boulva and McLaren, 1979) whereas the seals in the present study were fed mid day. Also, as Tester (1987) proposed, their breeding behaviour seems to have affected this rhythm. Changes in daily activity patterns were seen before and after mating. Before mating, both males did not show reduced activity from 6PM to midnight which was in evidence after mating. This was probably because most flipperslapping and bubbleblowing occurred at this time before copulation had occurred.

4.2. SOCIAL INTERACTION

This study is the first to provide a detailed description of copulation and the events preceding it in (*Phoca vitulina*). Although it has never been observed in the wild, Beier and Wartzok (1979) described mating in a pair of captive spotted seals *Phoca largha*. Their observations were similar to those in the present study in that copulation was *more canem*. It occurred for several minutes, with the pair sinking beneath the the water and coming back to the surface again. Multiple copulations were not described in the spotted seal, however in harbour seals, male 1 and the female copulated at least three times.

The two adult males engaged in flipperslapping and bubbleblowing just prior to copulation, and seldom thereafter. Venables and Venables (1957) and Scheffer and Slipp (1944) suggested that these activities may be a form of courtship. They reported that these behaviours were only seen in males and they occurred in July and August near the time of breeding. Others have reported observations of aquatic courtship in male Weddell seals *Leptonychotes weddelli* (Kenyon and Rice, 1959). The fact that in the present study these behaviors occurred prior to

copulation but were rarely observed after this period suggests that they function as reproductive displays. Since flipperslapping is audible over long distances, underwater, and in air it would be an effective way for male harbour seals to communicate and display to females. These two behaviours were never observed in the female or younger animals. Male 1 engaged in these behaviours more than male 2 (Table 3-8 and Table 3-9) and this may have been in some way related to his reproductive success. Beier and Wartzok (1979) reported an increase in spotted seal *Phoca largha* interactions and vocalizations for a two week period prior to mating, however no change in overall activity levels were seen during this time. This is contradictory to the findings in this study, since both males showed an increase in activity prior to copulation. Beier and Wartzok (1979) however, did not report any behaviours similar to flipperslapping and bubbleblowing.

Stirling (1975) proposed that male weddell seals formed underwater territories. The results in the present study suggest that these seals may show space preferences (Table 3-10 and 3-11). Male 1 displayed in quadrant 2 for the most part while male 2 displayed in quadrant 4. Significant differences are seen before and after the mating period in that restriction on their use of space disappears. Before mating, male 1 performed nearly all of his displays in quadrant 2 whereas male 2 displayed mostly in quadrant 4. After mating, male 2's longest display bouts were in quadrants 1 and 2. Perhaps he did not enter this space before mating because male 1 somehow excluded him. Since there was no evidence of agonistic behaviour throughout the study, the likelihood of such exclusion seems low, unless their displaying is by itself a foolproof means of avoiding aggressive encounters. Male 1 mated with the female and did not engage in any displays after this. Perhaps his "space" was no longer important and the fact that male 2 "intruded" during this time no longer mattered. The inherent value of quadrant 2 and quadrant 4 is not clear. Quadrant 2 is further from the tourist observation platform, and may be shielded somewhat from disturbances. Both males show a preference for swimming direction, male 1 swimming in a counterclockwise direction 70% of the time while male 2 swims in a clockwise direction 95% of the time. The findings that possible space preferences exist as well as a preferred swim pattern leads to the notion that the spatial arrangements of harbour seals

during the breeding season may not be as loosely organized as once believed (Wilson, 1978).

4.3. SLEEP

The two adult males were not observed to sleep for 7 days prior to copulation. After mating however, a marked increase in sleep was seen (Table 3-14). Male 1 slept the most in September (1034.50s) while male 2 slept the most in October (3497.20s). It seemed as if sleep somehow competed with more important activities (ie: pre-copulatory displays) in these animals and once mating was completed, sleep occurrences increased whereas aquatic displays ceased. Corresponding with an increase in sleep over the season was an increase in food consumption (Table 3-6). These animals may have been eating and sleeping in compensation for recent activities. The female, juvenile and pup were not observed sleeping in water until after copulation. They may have slept on land prior to this date but were not observed in the water until then. It is possible that the two adult males would not permit the other three seals to enter the tank prior to copulation.

The juvenile slept the longest on land while the female slept the least. Sleep durations were longer in water than on land for the adult animals suggesting that maybe harbour seals do not have to haul out to REM sleep or to conserve energy. Perhaps they can benefit from sleeping at the surface of the water just as well as if they were to haul out on land. Ridgway et al (1975) reported that grey seals could REM sleep at the surface of the water, however, storms at sea may prevent seals from sleeping and hence in the wild they may haul out to REM sleep. This study examined sleep on land for a short period (1 week). A more lengthy study is needed in order to draw conclusions and make comparisons about sleep on land in these animals. However, results from the previous summer revealed that 86% of their sleep time occurred on land and 14% in the water. This study included a larger N (8 seals versus 5), suggesting that seals who haul out in larger groups sleep longer. If this is true, it would support Terhune's (1985) findings as well as Schneider et al (1980) who believe seals may haul out to conserve energy. In a

large group, seals would not have to scan as frequently for predators and would have more time to rest and sleep. Scanning did not occur in the water in these animals. On land, however, scanning bouts were reported. When the seals in this study were observed scanning, they were either alone or in pairs. All five animals were not observed scanning at once. Scanning rates were only reported for a short interval of time and perhaps a more intensive study that encompassed the mating season would be appropriate. The greatest number of occurrences were seen by the juvenile and least number by the oldest. Renouf and Lawson (1985) reported an increase in scanning rates especially of adult males as mating drew near. It is possible that the animals in this study did not scan in a group because they are in captivity and there is no need to be concerned about predators. If the study had included the breeding season, the two adult males may have had high scanning rates. Both adult males and the juvenile spent a large proportion of time sleeping in quadrant 2 after mating. This is the quadrant where male 1 engaged in most of his pre-copulatory displays. If these animals are socially structured or exhibit "space" preferences, after the mating season they become more loosely structured and space is not so restricted.

At the outset, it was hoped that the study of this captive group might lead to hypotheses that can be tested in a wild population. More information is needed concerning the energetic parameters related to activity and food consumption. Most data on food consumption is provided by either scat or stomach analysis which does not give a good indication of food ingested over time (Murie and Lavigne, 1985). This study of captive animals allowed changes in food consumption to be monitored continuously and revealed that harbour seals show seasonal changes in food consumption and correlated changes in activity level. Perhaps in the wild, changes in activity might be a useful auxiliary index of food consumption.

More research needs to be conducted on the social behaviour of harbour seals. This study suggests that some sort of social structure may exist in these animals. The documentation of precopulatory displaying and the apparent restriction of space found in the present study suggest that some orderly form of social structure exists in harbour seals, which is aquatically based. Previous studies of

their social behaviour on land led some early worker's to suggest little or no social organization (Wilson, 1978). The present results indicate promise for studies in the wild of tagged and hence individually recognizable animals observed from a vantage point permitting behaviour in the water adjacent to their hauling grounds.

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APPENDIX 1a. STANDARD ERROR OF WEEK VERSUS ACTIVITY FOR EACH SEAL.

WEEK	MALE 1	MALE 2	FEMALE	JUVENILE	PUP
1	696.34	493.99	-----	-----	---
2	707.76	701.45	89.803	-----	---
3	471.71	431.29	352.10	53.74	49.50
4	298.37	327.63	216.45	21.00	291.43
5	376.47	262.09	253.86	43.84	95.86
6	169.86	289.90	229.47	106.77	218.33
7	404.50	298.27	217.22	190.41	211.00
8	166.36	268.66	131.34	3.22	91.03
9	276.53	108.29	176.34	145.00	124.90

APPENDIX 1b. STANDARD ERROR OF SAMPLE PERIOD VERSUS ACTIVITY FOR EACH SEAL.

SAMPLE PERIOD	MALE 1	MALE 2	FEMALE	JUVENILE	PUP
01	10.45	9.96	3.69	8.56	8.79
02	10.59	8.64	4.40	5.62	5.66
03	8.44	7.56	5.12	5.02	0.00
04	8.72	12.12	1.92	5.83	0.00
05	10.31	10.99	3.19	3.96	1.94
06	9.51	12.89	3.57	5.44	2.91
07	11.05	15.44	2.09	0.00	0.00
08	12.71	18.18	2.56	2.34	0.00
09	12.45	18.97	8.21	0.00	0.00
10	15.51	25.42	12.05	1.77	6.31
11	26.07	31.23	13.38	2.79	0.00
12	20.88	26.84	13.66	4.17	0.00
13	24.34	35.76	20.04	2.87	0.00
14	23.43	35.35	26.77	3.28	0.00
15	23.88	35.82	28.75	5.31	0.00
16	28.12	33.47	29.83	9.65	0.00
17	29.70	30.87	31.17	11.26	3.70
18	28.91	27.54	28.18	11.91	2.00
19	27.93	28.50	25.47	13.37	8.52
20	24.75	28.22	25.59	18.07	7.35
21	25.33	27.78	26.90	16.88	8.76
22	22.45	26.95	26.63	17.74	8.92
23	21.81	23.08	23.76	15.54	10.24
24	22.96	24.16	22.92	14.67	6.33
25	22.70	25.19	20.08	13.03	11.36
26	25.77	25.48	20.81	13.19	6.58
27	25.51	26.82	20.36	15.14	7.05
28	26.17	27.67	23.36	17.64	6.65
29	25.53	27.99	19.00	15.37	7.28
30	27.42	29.19	21.65	14.88	7.08
31	26.53	28.07	19.75	14.44	3.47
32	24.75	28.32	20.83	14.23	6.64
33	28.47	30.67	20.26	16.40	4.19
34	26.57	28.56	16.88	14.77	4.86
35	24.99	29.96	15.97	16.66	5.78
36	23.61	23.50	17.77	16.08	6.73
37	28.66	28.91	17.06	20.63	2.08
38	30.16	27.19	18.72	21.77	1.80
39	29.91	26.98	17.31	18.89	2.07
40	28.65	25.85	16.30	14.02	2.58

41	24.78	20.60	16.39	5.08	6.41
42	22.17	20.99	14.41	5.70	2.07
43	18.43	18.58	12.23	9.08	9.19
44	17.24	15.67	5.82	7.57	3.87
45	15.72	11.56	5.26	7.61	2.32
46	10.89	9.60	6.91	3.92	3.21
47	13.98	11.51	10.10	3.84	9.73
48	13.03	10.31	11.75	2.43	3.33

